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The Altered Gravitropic Response of the *lazy-2* Mutant of Tomato Is Phytochrome Regulated[1]

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Shoots of the *lazy-2* (*lz-2*) gravitropic mutant of tomato (*Lycopersicon esculentum* Mill.) have a normal gravitropic response when grown in the dark, but grow downward in response to gravity when grown in the light. Experiments were undertaken to investigate the nature of the light induction of the downward growth of *lz-2* shoots. Red light was effective at causing downward growth of hypocotyls of *lz-2* seedlings, whereas treatment with blue light did not alter the dark-grown (wild-type) gravity response. Downward growth of *lz-2* seedlings is greatest 16 h after a 1-h red light irradiation, after which the seedlings begin to revert to the dark-grown phenotype. *lz-2* seedlings irradiated with a far-red light pulse immediately after a red light pulse exhibited no downward growth. However, continuous red or far-red light both resulted in downward growth of *lz-2* seedlings. Thus, the light induction of downward growth of *lz-2* appears to involve the photoreceptor phytochrome. Fluence-response experiments indicate that the induction of downward growth of *lz-2* by red light is a low-fluence phytochrome response, with a possible high-irradiance response component.

There are several reports in the literature of an interaction between light and the gravity response of higher plants. The clearest and best-studied example of such an interaction is the phytochrome-regulated switch from a diagravitropic growth habit of dark-grown roots of the Merit variety of corn to a positive gravitropic growth habit after R irradiation (Mandoli et al., 1984). The same response has been reported in other varieties of corn (Johnson et al., 1991) and in *Convolvulus arvensis* (Tepfer and Bonnett, 1972). Feldman and Briggs (1987) demonstrated that the phytochrome response of Merit was a VLFR.

Data on the interactions between phytochrome and the gravitropic response of shoots are conflicting. Kang and Burg (1972) reported a stimulation of the gravitropic response of peas after R irradiation. On the other hand, there are reports of R irradiation resulting in an inhibition of gravitropic curvature in peas (McArthur and Briggs, 1979) and watercress (Hart and MacDonald, 1980). Another study (Britz and Galston, 1982) concluded that R pretreatment enhanced gravity perception but that, ultimately, the kinetics and extent of the gravitropic response were identical in R-irradiated and dark-grown control plants. Thus, although it appears that phytochrome can modulate the shoot gravitropic response in some plants, the exact nature of the light/gravity interaction is unclear.

Here we report on the *lz*-2 gravitropic mutant of tomato (*Lycopersicon esculentum* Mill.), for which exposure to light results in a specific reversal in the direction of the shoot gravitropic response. In the dark, *lz*-2 plants exhibit a typical gravitropic response: differential growth leads to an upward reorientation of the shoot apex and a downward reorientation of the root apex. However, when plants carrying the *lz*-2 mutation are placed in the light, the stem response is reversed so that the shoot apex becomes reoriented downward (Roberts, 1987) but the root response is unchanged (Gaiser and Lomax, 1992). If the *lz*-2 plants are returned to the dark, they revert to the wild-type phenotype, exhibiting upward reorientation of the shoot apex (Roberts, 1987).

We have previously shown that light-induced downward curvature in *lz*-2 is a directed response to gravity rather than simply a failure to grow upright (Gaiser and Lomax, 1992). Shoots of *lz*-2 seedlings apparently sense the gravitropic vector normally, but respond in the opposite direction than do wild-type plants. *lz*-2 seedlings show no variation from wild type in their elongation response to exogenous IAA and are able to carry out B-mediated phototropic curvature in the proper direction (Gaiser and Lomax, 1992).

Light-induced downward growth of *lz*-2 stems is enhanced by R as compared with W (Gaiser and Lomax, 1992; Roberts and Gilbert, 1992). We demonstrate here that this downward growth is regulated by the photoreceptor phytochrome. Our data from experiments with dark-grown *lz*-2 seedlings suggest that (a) whereas R is capable of inducing the *lz*-2 mutant phenotype (downward growth of stems), B is not; (b) an FR pulse reverses the effect of an R pulse, but both continuous R and FR are capable of causing downward growth; and (c) other phytochrome-regulated photomorphogenic responses appear normal in *lz*-2. Taken together with fluence-response measurements, the data suggest that downward growth of *lz*-2 seedlings is an LFR with a possible HIR component.

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Abbreviations: B, blue light; FR, far-red light; HIR, high irradiance response; LFR, low fluence response; *lz-2*, *lazy-2*; R, red light; VLFR, very low fluence response; W, white light.

MATERIALS AND METHODS

Plant Material

Wild-type (cv Ailsa Craig) and *lz-2* tomato (*Lycopersicon esculentum* Mill.) seeds were originally supplied by Dr. C.M. Rick of the University of California, Davis. *lz-2* is an ethyl methanesulfonate-induced, monogenic recessive mutation originally isolated in tomato cv San Marzano by Sorressi and Cravedi (1967) and subsequently backcrossed into Ailsa Craig. Seeds were soaked in 20% (v/v) bleach for 15 min, rinsed well with tap water, and sown onto Petri plates lined with water-saturated, unbleached paper towels (Kimtowels, Kimberly-Clark Corp., Roswell, GA). The plates were sealed with parafilm (American National Can, Greenwich, CT), wrapped in aluminum foil, and incubated in the dark at 28°C until use.

Scoring Method for Downward Growth

Four- to 5-d-old dark-grown seedlings were measured with a ruler and calipers. Only seedlings with hypocotyl lengths of 4 to 11 mm from the crest of the hook to the root/shoot junction were used in experiments; all other seedlings were removed. Seedling populations were normalized so that each plate contained an equivalent distribution of seedlings within the 4- to 11-mm range. The seedlings were maintained in light-tight boxes lined with water-saturated Kimtowels except during manipulations, which were performed as rapidly as possible under dim overhead green light (<0.05 μmol m^{-2} s^{-1} at seedling level). Each plate of seedlings was used for only one timepoint.

After light treatment, downward growth was visually quantitated. A seedling was scored as exhibiting "downward growth" if the apical region was reoriented at an angle ≥90° from vertical, as in the R-irradiated *lz-2* seedlings in Figure 1. The percent of the seedling population exhibiting downward growth was calculated as (number of seedlings exhibiting downward growth/total number of seedlings in population) ×100. This technique has two distinct advantages over others that were tried. First, the orientation of the seedlings with respect to the gravity vector is not altered during the course of the experiment; that is, light was the only environmental variable tested in these experiments. Second, by scoring downward growth using the above criteria, the possibility of scoring false positives due to nutation was eliminated.

Light Sources

R was provided by two overhead fluorescent tubes (40 W Shoplight, General Electric) filtered through red acrylic (Shinkolite 102, Argo Plastics Co., Los Angeles, CA). The R fluence rate was adjusted by varying the distance between seedlings and light source. Fluence rates used were: 40.0 μmol m^{-2} s^{-1} (Fig. 2) and 20 μmol m^{-2} s^{-1} (Table I). The light source used for Figure 1 and the fluence-response curves (Fig. 3) was a microscope light equipped with a rheostat to vary fluence rate, a 750-W tungsten bulb (DDB, General Electric), and a Shinkolite filter. Fluence rates were measured with a Li-Cor quantum sensor (model Li-185A), which measures PAR.

FR was provided by the microscope light described above fitted with an FR filter (FRF700, Westlake Plastics Co., Lenni, PA). A radiometer was used to measure FR as W m^{-2} and converted to μmol m^{-2} s^{-1} using the energy of a photon at 710 nm. According to the manufacturer's specifications, approximately 80% of the light emitted from this filter is between 700 and 720 nm. The output from the FR source was adjusted with the rheostat. A fluence rate of 20 μmol m^{-2} s^{-1} was used for the continuous light experiment depicted in Table I.

B was obtained from one 35-W fluorescent tube (Westinghouse Cool White) filtered through blue acrylic (No. 2424, Denco Sales Co., Portland, OR). The B fluence rate was 1.0 μmol m^{-2} s^{-1} at seedling level.

For continuous W experiments, seedlings were incubated in a growth chamber (Hoffman Manufacturing, Albany OR) equipped with six 40-W Gro-Lux fluorescent tubes (Sylvania). The seedlings received W at a fluence rate of 20 μmol m^{-2} s^{-1}.

Anthocyanin and Chl Determinations

Anthocyanin and Chl were extracted from cotyledons essentially as described by Mancinelli et al. (1988) except that acidified (1% HCl, v/v) methanol was used at a rate of 30 mL g^{-1} fresh weight. The cotyledons were extracted for at least 6 h prior to reading the absorbance at 530 nm (peak absorbance of anthocyanin) and 657 nm (peak absorbance of Chl degradation products).

RESULTS

R Induction and FR Reversal of Downward Growth in *lz-2* Seedlings

The gravitropic responses of wild-type and *lz-2* seedlings under two different light conditions and in the dark are shown in Figure 1. *lz-2* seedlings have a wild-type response to gravity when grown in the dark. However, continuous R irradiation induces a reversal of the gravitropic response of *lz-2* shoots, leading to downward growth, but does not affect the direction of the wild-type gravitropic response. B does not alter the gravitropic response of either wild-type or *lz-2* seedlings. Possible confusion of phototropism with B-induced downward growth was avoided by placing the B-irradiated seedlings on a rotating platform to continually change the light vector without altering the gravity vector. Dark-grown and R- and B-irradiated wild-type and *lz-2* seedlings are morphologically similar and exhibit no obvious differences in hook conformation, cotyledon expansion, or root morphology.

To test whether the R induction of downward curvature in *lz-2* was reversed by FR, dark-grown (4-d-old) wild-type and *lz-2* seedlings received either 0.5 h of FR followed by 0.5 h of R or the reverse. Both light sources emitted 40 μmol m^{-2} s^{-1}, and the plants were scored for downward growth 23 h after the light treatment. No downward growth occurs in wild-type tomato seedlings with either light regimen or in the dark controls. In contrast, 56.3 ± 5.1% of the *lz-2* seedlings exhibit downward curvature when R was given last. However, if the R irradiation was followed by an FR irradiation, no downward growth was observed (data not shown).

Kinetics for Downward Growth following an R Pulse

To determine the time required for maximal downward growth, dark-grown *lz-2* and wild-type seedlings were given a 1-h R irradiation and then returned to the dark. The number of seedlings exhibiting downward growth was recorded at various times postirradiation, as shown in Figure 2. Downward growth was maximal 16 h after the R irradiation. After more than 16 h in the dark, a gradual decrease in the percentage of seedlings exhibiting downward growth was observed due to reversion to the dark-grown phenotype.

Although *lz-2* seedlings grow downward after the R irradiation and wild-type seedlings do not, there was no difference in overall hypocotyl length in the experiment depicted in Figure 2 (data not shown). In fact, at the fluences that here induce downward growth in *lz-2*, we observe no R-induced inhibition of hypocotyl elongation in either wild-type or *lz-2* seedlings (although this response is observed in the continuous irradiation experiments depicted in Table I). Therefore, it is likely that downward growth in *lz-2* seedlings is not due to a drastic change in overall growth rate, but rather to an alteration in relative growth rates on either side (or both sides) of the hypocotyl.

Induction of Downward Growth as a Function of Fluence

We have determined the downward curvature of *lz-2* seedlings as a function of R concentration. Figure 3 shows the results of experiments in which seedlings were irradiated with various fluences of R, returned to the dark for 16 h, and then assayed for percent induction of downward curvature. To understand better the relationship between R fluence rate and time of irradiation in the ability to initiate downward growth in *lz-2*, the R fluence was modulated in two ways. First, the fluence rate was kept constant at 40 μmol m^{-2} s^{-1} and the time of irradiation was adjusted (Fig. 3, curve A) to achieve the various fluences indicated. Second, the time of irradiation was kept constant at 5000 s while the fluence rate was adjusted (Fig. 3, curve B). Overall, the fluence-response curves of Figure 3 are similar. The percentage of seedlings exhibiting downward growth increases with increasing fluence of R to approximately 35% at 10^5 μmol m^{-2} with either constant time of irradiation (curve B) or constant fluence rate of R (curve A). However, the threshold of induction of downward growth differs in the two curves by one-half order of magnitude of R fluence. It appears that in the fluence range of 10^2 to $10^{3.5}$ μmol m^{-2}, a brighter, shorter irradiation (curve A) is more effective at inducing downward growth than a dimmer, longer irradiation (curve B). At fluences between 10^4 and 10^5 μmol m^{-2}, the percent induction of downward growth is identical regardless of which R regimen is used. This suggests that reciprocity is valid over this range of fluences.

The difference in the percent of *lz-2* seedlings exhibiting downward growth at 10^6 μmol m^{-2} of R is most likely due to the difference in time of irradiation at this fluence between the two experiments (25,000 s in curve A versus 5,000 s in curve B). This is illustrated by data from experiments in which seedlings were irradiated with three pulses of 200 μmol m^{-2} s^{-1} R. The duration of the pulses was varied to obtain a desired fluence, but were always evenly spaced over 15,000 s. Downward growth was scored 16 h after the final pulse. A 2-fold increase in the percent of *lz-2* seedlings growing downward is observed when a given fluence of R is administered over 15,000 s as compared with the same fluence given over 5,000 s (data not shown). A greater response with longer irradiation times is characteristic of an HIR (Mancinelli and Rabino, 1978).

Effect of Continuous Irradiation on *lz-2*

To test if there is an HIR component in the phytochrome regulation of the *lz-2* phenotype, as suggested by the fluence-

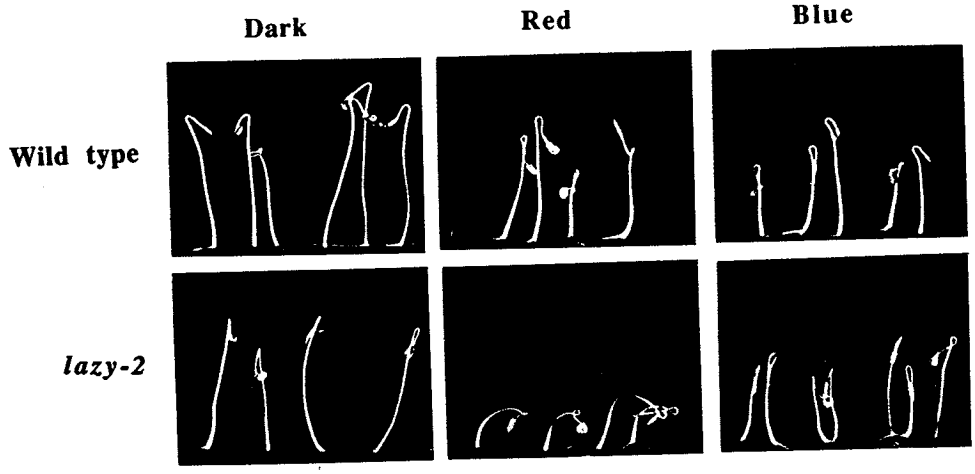

Figure 1. Effect of light quality on downward growth of *lz-2* seedlings. Dark-grown, 4-d-old wild-type and *lz-2* seedlings were irradiated overnight in R or B or maintained in the dark. Both the B source and R source provided illumination from the side. Phototropism was eliminated by placing the B-irradiated seedlings on a rotating platform to continually alter the light vector. The similar direction of curvature of the R-irradiated *lz-2* seedlings was artificially arranged. The direction of curvature of *lz-2* seedlings is random. Apparent variation in hook tightness is a result of camera angle rather than actual phenotypic differences. The fluence rate from both light sources was 1.0 μmol m^{-2} s^{-1}.

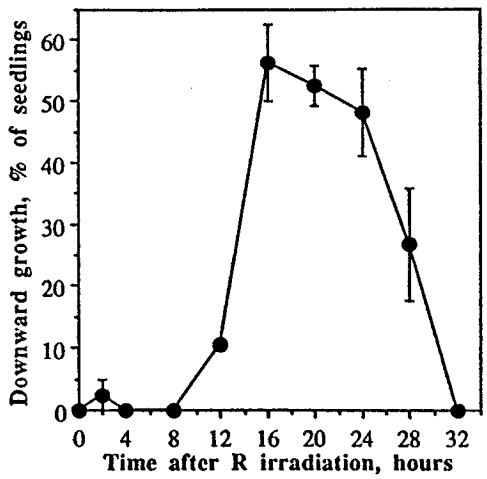

Figure 2. Kinetics for downward growth following an R irradiation. Dark-grown *lz-2* seedlings with a hypocotyl length of 4 to 11 mm were irradiated with R for 1 h (total fluence 7.2×10^4 μmol m^{-2}) and then returned to the dark. Downward growth was scored at the postirradiation times indicated. From three to eight experiments with 10 to 30 seedlings per experiment were completed for each timepoint. The SE values from these experiments are indicated.

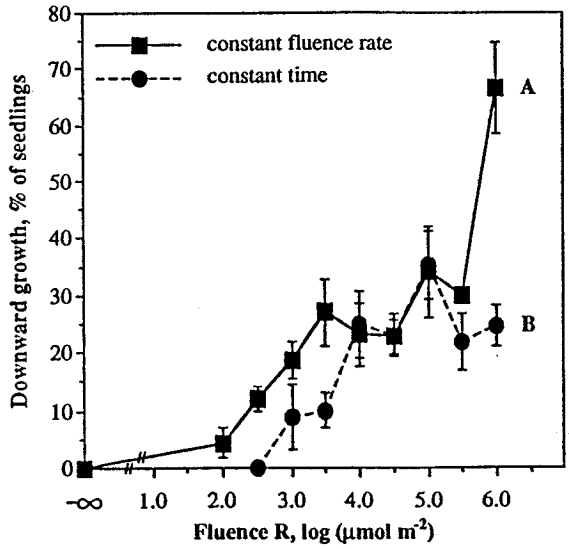

Figure 3. Fluence-response curves for downward growth of *lz-2* seedlings. *lz-2* seedlings were irradiated with R (fluence rate 40 μmol m^{-2} s^{-1}) for varying lengths of time (A), or with R of various fluence rates for 5,000 s (B), to obtain the indicated fluences of R. The seedlings were returned to the dark for 16 h and then scored for downward growth. The irradiation times used for curve A were 2.5, 7.9, 25, 79, 250, 790, 2,500, 7,910, and 25,000 s. The fluence rates used for curve B were 0.06, 0.2, 0.63, 2.0, 6.3, 20.0, 63.0, and 200.0 μmol m^{-2} s^{-1}. From 3 to 10 experiments were performed for each fluence. The SE values of these experiments are indicated.

response curves presented in Figure 3, we irradiated *lz-2* and wild-type seedlings in continuous R, FR, and W. As can be seen in Table I, all three light conditions induced downward growth in *lz-2* seedlings but had no effect on the direction of the wild-type gravity response. The small percentage of *lz-2* seedlings grown in FR or W that were not scored as exhibiting downward growth was a result of the stringent scoring method. Although the apex was not reoriented to ≥90° from vertical in these plants, all of the *lz-2* seedlings in any of the light conditions in Table I exhibited some degree of downward curvature. Because continuous FR is capable of causing downward growth of *lz-2* seedlings, it is possible that the fluence-response curves in Figure 3 are a composite of two responses: an LFR at short irradiation times where reciprocity is valid and FR is capable of reversing the R induction of downward growth, and a HIR at long irradiation times where there is reciprocity failure and induction of the response by continuous FR.

Mutants with reduced phytochrome A levels, such as the tomato *aurea* (*au*) mutant (Parks et al., 1987), or reduced phytochrome B levels, such as the *elongated internode* (*ein*) mutant of *Brassica* (Devlin et al., 1992), do not accumulate wild-type levels of anthocyanin and Chl after FR or R irradiation, respectively (Koorneef et al., 1985; Devlin et al., 1992). The anthocyanin and Chl contents of *lz-2* seedlings were measured and found to be similar to wild type under all light conditions tested (Table I). Also, phytochrome mutants typically exhibit an elongated hypocotyl phenotype due to loss of phytochrome A, phytochrome B, or both (see Kendrick and Nagatani, 1991, for a review of phytochrome mutants). In contrast, the data in Table I show that *lz-2* hypocotyls are not significantly longer than wild-type hypocotyls after 2 d of continuous irradiation in R, FR, or W or

Table I. *Effect of continuous irradiation on lz-2 and wild-type seedlings*

Four-day-old *lz-2* and wild-type seedlings were irradiated with continuous R, FR, or W, or maintained in the dark. After 2 d, the seedlings were assayed for downward growth, hypocotyl length was measured, and the cotyledons were excised and used for anthocyanin and Chl determinations. The data represent the means from two separate experiments with 15 to 30 seedlings per experiment. The SE values are indicated.

	Anthocyanin		Chl		Hypocotyl Length		Downward Growth	
	Wild type	*lz-2*	Wild type	*lz-2*	Wild type	*lz-2*	Wild type	*lz-2*
	A_{530}/g fresh weight		A_{657}/g fresh weight		mm		% of population	
Dark	1.9 ± 0.1	1.9 ± 0.1	3.1 ± 0.3	3.1 ± 0.1	57.3 ± 2.4	57.3 ± 1.5	0.0 ± 0.0	0.0 ± 0.0
FR	2.6 ± 0.2	3.0 ± 0.3	4.3 ± 0.2	3.9 ± 0.0	57.7 ± 5.5	49.4 ± 0.0	0.0 ± 0.0	86.6 ± 0.9
R	12.6 ± 0.2	11.8 ± 1.2	46.5 ± 1.1	44.2 ± 3.1	40.6 ± 0.9	40.1 ± 1.2	0.0 ± 0.0	100 ± 0.0
W	11.9 ± 1.5	12.9 ± 2.2	44.0 ± 2.9	47.1 ± 4.6	29.4 ± 1.1	28.1 ± 0.1	0.0 ± 0.0	92.3 ± 0.6

when maintained in the dark. Hypocotyl length was inhibited approximately 20% by R and 50% by W in both wild-type and *lz-2* plants.

DISCUSSION

It has previously been shown that R enhances the downward growth of *lz-2* seedlings (Gaiser and Lomax, 1992; Roberts and Gilbert, 1992). We have now characterized the light induction of the *lz-2* mutant phenotype, and we have determined that whereas R is capable of inducing downward curvature, B is not. We have also shown that an FR pulse administered immediately after an R pulse will completely reverse the R response. This is strong evidence for the involvement of phytochrome in the regulation of the *lz-2* gene product.

To define further the control of the *lz-2* phenotype by phytochrome, we measured the kinetics of downward growth of dark-grown *lz-2* seedlings after an R irradiation. It should be noted that the data presented in Figure 2 are not a measure of the time required to initiate the change in growth after R irradiation. Indeed, the onset of seedling reorientation can be observed as early as 2 h after the R treatment (Gaiser and Lomax, 1992), but because these seedlings are curved less than 90° away from vertical, they are not scored as exhibiting "downward growth." Furthermore, when the seedlings are returned to the dark following the R pulse, reversion to the dark-grown phenotype begins. This was initially observed by Roberts (1987) for light-grown *lz-2* plants placed in the dark and is evident in the decrease in the percentage of seedlings growing downward 16 h after the R irradiation (Fig. 2). In fact, after 16 h, seedlings can be observed that have grown both downward and upward sequentially. These seedlings are not scored as growing downward (because their apical region is reoriented less than 90°), yet they clearly were growing downward at some time prior to scoring.

Phytochrome-regulated responses are often categorized as VLFR, LFR, or HIR based primarily on the amount of light required to elicit the response (see Smith and Whitelam, 1990, and refs. therein). The fluence-response curves (Fig. 3) most closely approximate those of an LFR, although the threshold for the R induction of downward growth is roughly 1 order of magnitude less sensitive to R than is typical (Smith and Whitelam, 1990). R doses below 10^2 μmol m^{-2} induce very little—if any—downward curvature of *lz-2* seedlings. That this response is photoreversible by FR is also indicative of an LFR. However, the large increase in downward growth of *lz-2* seedlings observed at 10^6 μmol m^{-2} (Fig. 3, curve A), which is due to duration of irradiation rather than absolute fluence, is characteristic of an HIR (for review, see Mancinelli and Rabino, 1978). High irradiance responses are characteristically elicited not only by R, but also by continuous FR. This is also true of downward growth in *lz-2* (Table I). It is possible, therefore, that the fluence-response curves in Figure 3 reflect a composite of two responses, an LFR and an HIR.

Phytochrome mutants exist that have reduced levels of phytochrome A (Parks et al., 1987; Parks and Quail, 1993) or phytochrome B (Somers et al., 1991; Devlin et al., 1992; López-Juez et al., 1992) or that are deficient in chromophore biosynthesis and therefore unable to synthesize photochemically functional phytochrome (Parks et al., 1989). In summarizing the literature, Parks and Quail (1993) conclude that phytochrome controls hypocotyl elongation through an FR-HIR response mediated by phytochrome A, and an R-HIR response mediated by phytochrome B. Therefore, plants carrying mutations in either phytochrome A or phytochrome B share a common phenotype, elongated hypocotyls, under continuous FR or R irradiation, respectively. In contrast to these mutants, *lz-2* hypocotyls are not significantly longer that wild-type hypocotyls after 2 d of continuous irradiation in R, FR, or W (Table I). Also, anthocyanin and Chl levels, which are often greatly reduced in phytochrome mutants, are similar in *lz-2* and wild-type seedlings under all light conditions tested. Furthermore, *au*, a tomato phytochrome A mutant, exhibits a suite of obvious photomorphogenic aberrations, including pale yellow foliage and drastically reduced seed germination (Koorneef et al., 1985); none of these aberrations are present in *lz-2* plants. Therefore, we feel it is unlikely that the *lz-2* mutation affects the phytochrome molecule itself. However, it is conceivable that *lz-2* represents a new class of phytochrome mutant. Recent research has made it clear that different forms of phytochrome control different aspects of photomorphogenesis (Adamse et al., 1988; Smith and Whitelam, 1990; Kendrick and Nagatani, 1991), and perhaps some form of the photoreceptor molecule itself is altered in *lz-2*, resulting in the aberrant gravitropic response.

We feel it is more likely that the *lz-2* mutation is in a gene that affects some step subsequent to the photoreceptor. Perhaps the *lz-2* lesion involves an intersection point between the light- and gravity-response mechanisms (see Roux and Serlin, 1987). In this context, Kelly and Leopold (1992) have presented evidence that in the Merit cultivar of maize, R is not required for the early steps of gravitropism (i.e. perception) but rather modulates or enhances later steps, leading to an altered growth response. This is in accordance with our hypothesis that the *lz-2* gene product is involved subsequent to gravity perception in gravitropic signal transduction (Gaiser and Lomax, 1992). It is interesting to note that R decreases the amount of IAA present in the epidermis of both dicots (Behringer and Davies, 1992) and monocots (Jones et al., 1991). Jones and co-workers analyzed IAA transport in R and in darkness and came to the conclusion that the R-induced decrease in IAA was due to an alteration of IAA transport. Therefore, it is possible that R induces a change in IAA transport in *lz-2* such that IAA redistribution (lateral transport) during gravitropism is reversed or altered, leading to downward curvature. However, at this stage other mechanisms such as changes in hormone sensitivity or alterations in an inhibiting compound cannot be excluded.

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